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RESEARCH PAPER

Dwarf shrubs may mitigate the negative effects of climate change on spiders by moderating microclimate

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ABSTRACT

Climate change negatively affects arthropod biodiversity worldwide. Mitigating the resulting arthropod decline is a great challenge. Dwarf shrubs in open areas might buffer microclimatic extremities by reducing the solar radiation reaching the ground and weakening air circulation near the soil surface. Forest steppes are mosaics of forests and grasslands covering a vast area in Eurasia. This heterogeneous ecosystem offers the opportunity to study the effect of small habitat features, i.e. dwarf shrubs, in dry grasslands and compare the fauna of rosemary-leaved willow (*Salix rosmarinifolia*) shrubs with forest patch interiors, open grasslands and their edges. We hypothesized that the dwarf shrub microhabitat has a wetter and cooler microclimate than open grassland and a different spider community composition than other forest-steppe microhabitats. We recorded microclimatic parameters with data loggers, measured soil moisture with TDR and collected ground-dwelling spiders with pitfall traps. We detected the highest soil moisture (6.26 ± 1.21%, mean ± 95% confidence interval) and air humidity (80.19 ± 3.19%) in forests and the lowest in grasslands (4.36 ± 0.65%; 66.59 ± 2.53%, respectively). The warmest microhabitats were grasslands (23.23 ± 0.51°C), whereas the coolest microhabitats were forests (18.92 ± 0.41°C). The distinct microclimate of dwarf shrubs was cooler (21.46 ± 0.41°C) and moister (5.43 ± 0.53%) than the surrounding semi-desert like grassland. Furthermore, we found a different spider community composition and trait state composition of spiders in forests, edges, grasslands and dwarf shrub microhabitats. Forests (9.90 ± 0.95) and edges (11.44 ± 1.27) hosted a higher species richness than grasslands (7.08 ± 4.27) and dwarf shrubs (5.09 ± 1.33). We collected larger spiders on the edges than in dwarf shrub microhabitats. The dwarf shrubs hosted a different microclimate and spider community composition from the grassland. Climate change in the forest-steppe region is assumed to be driven by a combination of warming and drying. In the coming decades, drought frequency and severity are predicted to increase. Woody vegetation, even dwarf shrubs, creates a thermal and moisture heterogeneity that might aid arthropods in buffering macroclimatic warming through behavioural thermoregulation. Therefore, their presence on grasslands can benefit the conservation of specialised grassland arthropods.

Introduction

Climate change has been responsible for insect declines in the last century, besides many principal stressors, including land-use change by agricultural intensification and urbanisation, invasive species, and pollution. Climate change influences arthropods in many ways. It may induce shifts toward earlier seasonal activity, prolong activity periods of many species and alter species' interactions by decreasing the synchronisation between arthropods and their food (Forrest, 2016). It may also trigger range shifts of arthropods toward cooler climates as species track their thermal requirements (Laws, 2017). (Wagner et al., 2021; Müller et al., 2024).

Understanding the drivers of arthropod diversity and mitigating arthropod decline is a great challenge. At the local scale, the role of habitat heterogeneity has long been recognised to affect arthropods (Joern & Laws, 2013). Thermal heterogeneity of fine-scale climate variations between microhabitats allows arthropods to buffer thermal extremes by moving between microhabitats (Pincebourde & Woods, 2020). Furthermore, the habitat heterogeneity hypothesis states that species diversity increases with habitat complexity, assuming that

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microhabitat types are heterogeneous within a habitat (Simpson, 1949, Pianka, 1966, MacArthur, 1972). Complex habitats may provide more niches and diverse ways of exploiting the resources (Tews et al., 2004). Vegetation in grasslands serves as the physical habitat for most arthropods. Therefore, vegetation attributes, such as heterogeneity of structural architecture, can influence arthropods (Joern & Laws, 2013). Most published studies found a positive relationship between habitat heterogeneity and arthropod diversity (Wong et al., 2019). Still, the results vary between ecosystems and focal arthropod taxa, as not all species in an ecosystem are equally affected by vegetation structures (Tews et al., 2004).

The abiotic conditions differ markedly between short and tall vegetation. Short vegetation leads to a dry and warm microclimate with high soil temperatures favouring xerotolerant and thermophilous arthropods. In contrast, tall vegetation buffers the microclimate, such as extreme temperature fluctuations and drought (Roy & Thomas, 2003, van Klink et al., 2015). Tall vegetation is generally accompanied by a dense litter layer due to the large biomass production, increasing the abundance of detritivores and their predators (Langellotto & Denno, 2004).

Woody structural elements, such as dwarf shrubs, may affect the ecosystems in many ways. For example, shrubs may stabilise the soil surface by reducing wind erosion (Zhang & Zhao, 2015). Furthermore, trees and shrubs modify their microhabitat parameters. They could moderate the effects of global warming on grassland arthropods by reducing ground surface temperatures (Asmus et al., 2018, Brigham & Suding, 2023). Dwarf shrubs in open habitats reduce the solar radiation reaching the ground and weaken air circulation near the soil surface. Therefore, they may create a cooler microclimate during the hot summer and could modulate the effects of global warming on arthropods (Asmus et al., 2018).

Soil moisture and air humidity might be decreased by canopy interception of precipitation (Zhang et al., 2016). Furthermore, the larger leaf surface of dwarf shrubs compared to grassland plants may lead to increased evapotranspiration (Zwieback et al., 2019, Kemppinen et al., 2021). Therefore, soil moisture might be lower in dwarf shrub microhabitats than in the surrounding open areas, as found in northern tundra (Bonfils et al., 2012, Kemppinen et al., 2021). However, dwarf shrubs may also increase soil moisture by hydraulic lift during the night and improve soil resources for plants through litter accumulation, and leaf litter may also retain the soil moisture content (Gonzalez & Ghermandi, 2019). Microclimatic conditions of small-scale habitat structures affect spider communities (Barton et al., 2017). The reduced temperature and increased soil moisture support a range of species that cannot establish viable populations on grassland. Furthermore, dwarf shrubs may provide extra food resources and spatial structure for herbivore arthropods that serve as food items for arthropod predators, such as spiders (Birkhofer et al., 2010). Therefore, dwarf shrubs may have a disproportionately strong effect on the species richness and composition of arthropods (Barton et al., 2009, Gallé et al., 2023).

Forest steppes are mosaics of grassland intermixed with forests covering large areas in Eurasia. This heterogeneous habitat in Central Hungary was developed on sandy soil. Forests generally occupy 10–20% of the forest steppes and consist of dense trees and shrubs (e.g. *Populus alba, Crataegus monogyna, Juniperus communis*). Forest patches are known to reduce environmental harshness, with specialised flora (Bátori et al., 2018) and arthropod fauna (Gallé et al., 2022, Hamřík et al., 2023), with the highest species richness at the edges (Bátori et al., 2018). Grassland vegetation consists of drought-tolerant plant species (e.g. *Alkanna tinctoria, Festuca vaginata* and *Stipa borysthenica*). The dwarf shrub, rosemary-leaved willow (*Salix rosmarinifolia*) occurs in the grassland component of the forest steppe. This dwarf willow forms microhabitat patches with a diameter reaching 3 m and a maximum height of 50-70 cm. This mosaic ecosystem offers a unique opportunity to study the effect of microhabitat features, i.e. dwarf shrubs, in dry grasslands and compare the fauna of rosemary-leaved willow with forest edges, forest interiors and open grasslands.

Spiders are among the most important arthropod predators in terrestrial ecosystems. They depend on the vegetation indirectly via microclimate and the consumption of herbivores and directly by the physical structure, a substrate for vegetation-dwellers and providing web attachment points (Dennis et al., 2015). Spiders have outstanding dispersal abilities using passive airborne ballooning. Therefore, they can rapidly colonise habitats that recently became favourable (Weyman, 1993). Spider communities can have a high trait state diversity in structurally complex microhabitats (Schirmel et al., 2012). Focusing on spider traits besides species richness may help the mechanistic explanation of changes in community composition (Buchholz, 2010a).

Vegetation-moderated effects of microclimate on arthropod diversity by small vegetation structures, such as dwarf shrubs are overlooked, despite their importance and prevalence in many habitats worldwide (Urák et al., 2023; Brigham & Suding, 2023). In this study, we focus on the effect of the dwarf shrub, rosemary-leaved willow, on the microclimate and the spider fauna in mosaic forest steppes. We hypothesise that (1) dwarf shrubs are important microhabitats, with moister and cooler microclimate than open grasslands. (2) The presence of shrubs increases species richness and changes the community composition of grasslands. (3) As dwarf shrub affects trait-state composition of spider assemblages, we would find more vegetation dwellers in dwarf shrub microhabitats than in open grasslands, due to the complex structure of the shrubs. (4) Furthermore, we expect spider species to follow the microclimatic gradient. Therefore, we would collect fewer shade-tolerant and more xerotolerant species in the dwarf-shrub microhabitats than in the forests and edges, but more than in the open grasslands.

Materials and methods

Study region and site selection

We conducted a study in the Southern part of the Hungarian Great Plain, 120-150 m a.s.l. This region has a continental climate with a mean annual temperature of 11 °C and a mean annual precipitation of 550-600 mm. The natural vegetation here was sandy forest-steppe, a dynamic mosaic of forested patches consisting of *Populus alba* L., Crataegus *monogyna* Jacq. with a maximum area of a few hundred square metres, and dry bunchgrass steppes dominated by *Festuca vaginata* Waldst. & Kit. ex Willd and *Stipa borysthenica* Klokov ex Prokudin (Fig. 1). The proportion of woody vegetation was between 10 and 30% (Gallé et al., 2023). Natural vegetation remains in fragments surrounded mainly by forest plantations of exotic (black locust, pines) and native (poplar) tree species with 42% forest cover surrounding the study area (Gallé et al., 2022' Nébih, 2024). We selected and established study sites in 12 fragments (mean ± 95% CI: 203 ± 108 ha) in the vicinity of the villages Kéleshalom (1), Pirtó (2) and Tázlár (3) with a minimum distance of 500 m between them. At each study site, we sampled forests, forest edges, grasslands and dwarf shrubs. We identified relatively large forest patches, all sampled forest patches were larger than 500 m^2. Sampled microhabitats were at least 20 m apart. We measured the length (167.2 ± 59.6 cm, mean ± SD), width (126.6 ± 46.2 cm) and height (43.2 ± 22.9 cm) of dwarf shrubs and calculated their volume, which ranged between 0.07 m^3 and 3.02 m^3 (0.61 ± 0.67 m^3).

Soil moisture and microclimate measurements

We measured soil volumetric moisture content in the upper 20 cm at 10 random points in each microhabitat on two occasions on 24th May and 28th June 2022, with no rainfall in the preceding three days with a Field Scout TDR 350 soil moisture meter (resolution: 0.1 V/V% of water). We obtained 960 soil moisture data values (12 forest-steppe fragments × 4 microhabitats × 10 measurements × 2 temporal replicates), and averaged the data per fragment per microhabitat. We assessed the air temperature using data loggers (Optin ADL TH3-32) by

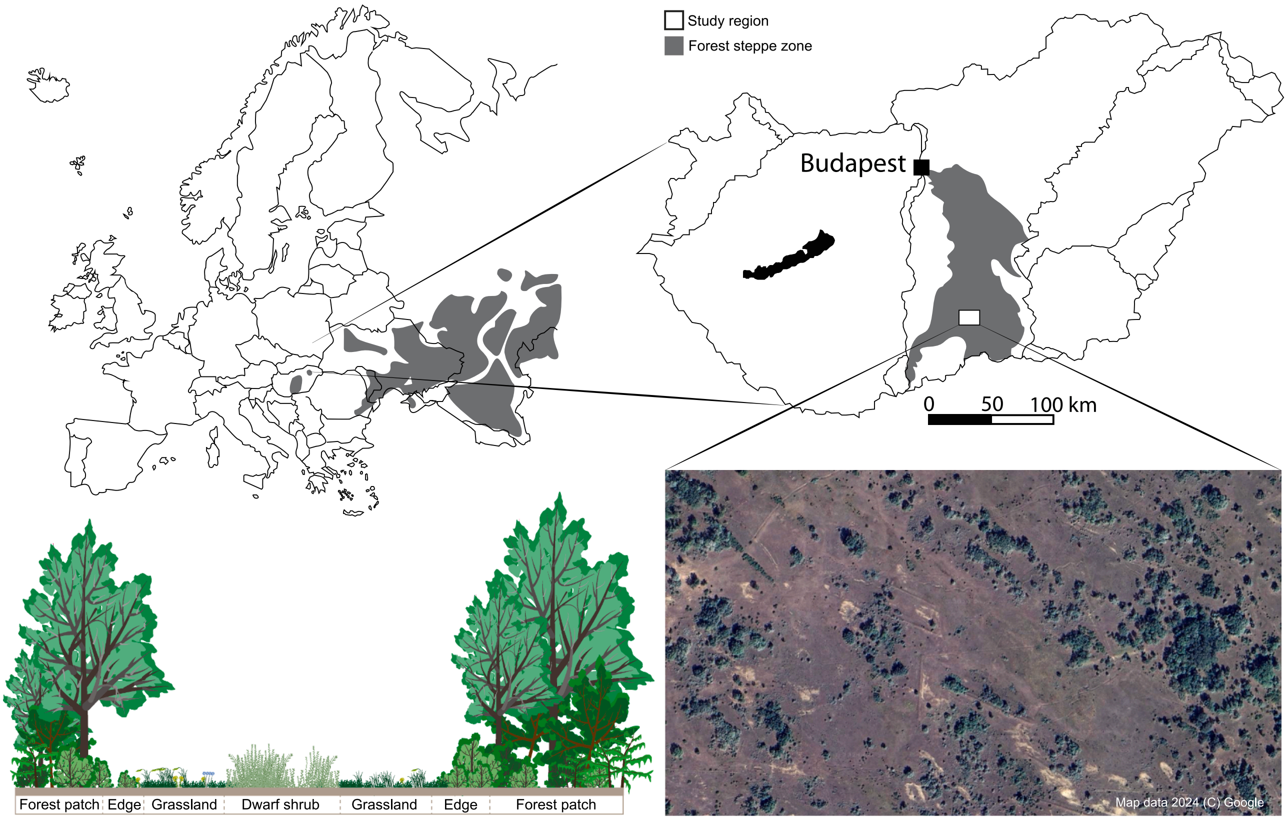

Fig. 1. Location of the sampling region in Hungary, a cross-section of a forest-steppe mosaic and a satellite image of a forest steppe mosaic.

installing one logger in each microhabitat and recorded microclimatic data every 20 minutes for 20 days between 25th May and 14th June 2022 in 9 randomly selected forest-steppe fragments. We limited our microclimate assessment due to the limited number of available data loggers (9 forest-steppe fragments × 4 microhabitats × 1data logger × 20 days × 96 measurements). We averaged air humidity, temperature, and daily maximum and minimum temperature data per fragment per microhabitat.

Spider sampling and identification

We used pitfall traps to collect spiders. We employed three traps in each sampling site (12 forest-steppe fragments × 4 microhabitats × 3 traps = 144 traps). Traps were 500-ml white plastic cups, 8.5 cm in diameter, we placed traps at least 8 m apart. We fitted the traps with transparent plastic funnels to reduce vertebrate bycatches and increase trapping efficiency (Császár et al., 2018). We filled them with 50% propylene–glycol and water solution containing a few drops of detergent to preserve the sample. We placed a plastic roof above each trap to prevent the dilution of the preservative. Traps were open for two weeks and repeated in two periods, between the 10th and 24th of May 2022 and the 14th and 28th of June 2022. We pooled the data from the two periods. We excluded traps if they were damaged at least in one of the sampling periods (7 traps), resulting in 137 statistical samples. All adult spider individuals were identified to species level using Nentwig et al. (2023).

Data analyses

We applied linear mixed-effect models (LMMs) to investigate the effect of microhabitat type on mean air humidity, temperature, and daily maximum and minimum temperatures in R (R Core Team, 2023). Our models included "microhabitat" as a fixed factor with four levels (forest, edge, grassland and dwarf shrubs). The fragment as sampling site ("site") nested in "village" was included as a random effect factor (LME4 package, Bates 2010). We applied model diagnostics following the protocol of Zuur et al. (2010). We used Tukey-type post hoc tests for pairwise comparison of microhabitats.

We used PERMANOVA tests with the Bray–Curtis distance measure to test the multivariate difference between spider communities of different microhabitat types with the vegan package (Oksanen et al., 2019). We transformed the species abundance data by Hellinger transformation before the tests to reduce the weight of species with high abundances (Legendre & Gallagher, 2001). If the PERMANOVA test detected significant differences between arthropod communities of the four microhabitats, we applied the indicator value analysis (IndVal) to identify characteristic species. We calculated the IndVal value based on the relative frequency and relative average abundance of the species we sampled. We considered a species as indicator if the calculated IndVal was higher than 0.25 (Dufrêne & Legendre, 1997). We visualised the community composition of spiders with non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measure and 100 random starts (Oksanen et al., 2019).

We classified spider species according to literature data based on their stratum, humidity and shade preference (Buchar & Ruzicka, 2002) and body size (Nentwig et al., 2023). We used five ordinal categories for stratum preference: Ground (code:1), herb (code: 2), shrub (code: 3), tree trunk (code: 4), canopy (5). We used five categories for humidity preference: drought-preferring (code: 1), dry habitat species (code: 2), species of semi-humid habitats (code:3), humidity-preferring species (code: 4), and species of very humid habitats (code: 5). Shading preference was classified into four categories: open habitat species (code: 1), species of semi-open habitats (code:2), species preferring partly shaded habitats (code: 3) and shade-preferring species. We averaged trait values if a species fell into more than one category. Body size was given for each species as a continuous variable and defined as the mean body length in

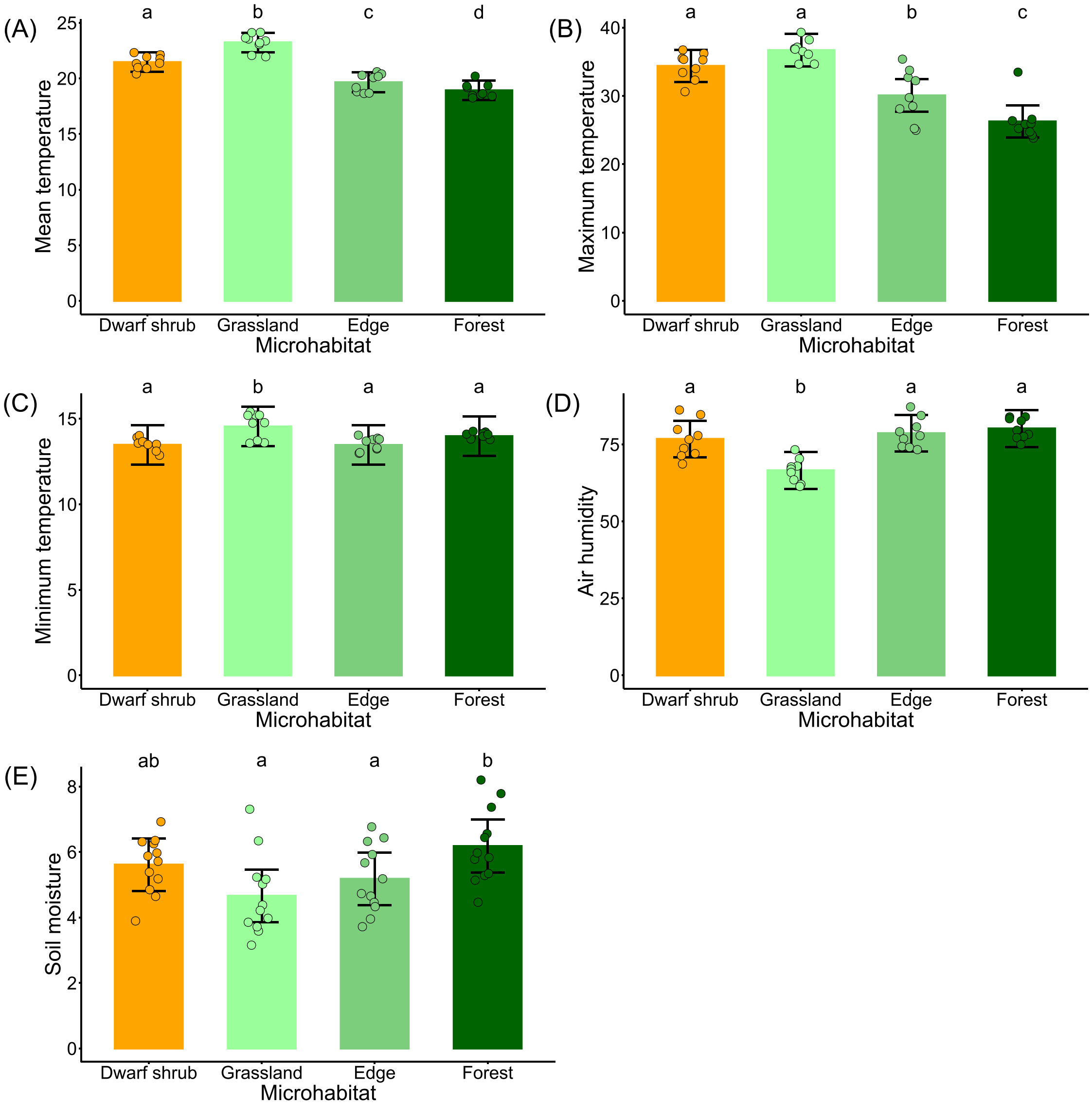

Fig. 2. Soil moisture and microclimatic parameters of microhabitat types. (A) Soil moisture (%), (B) mean air humidity (%), (C) mean temperature (°C), (D) mean of daily maximum temperatures (°C), (E) mean of daily minimum temperatures (°C). Bars represent estimated means; error bars are estimated 95% confidence intervals. Significant differences are indicated by different letters ($p < 0.05$).

millimetres averaged over males and females (see Appendix A).

We calculated community-weighted mean values (CWM) of all sampling sites and microhabitats with the "BAT" package (Cardoso et al. 2015). We ran a series of GLMMs with CWM values as response variables and microhabitat type as a fixed variable. To account for the spatial non-independence of our sampling sites, we used "site" nested in "village" as a random term. Furthermore, we studied the impact of microhabitat type on spider species richness with a general linear mixed-effect model (GLMM) with a "Poisson" error term with "site" nested in "village" as a random effect. We applied the same model diagnostics as in the case of microclimate variables.

Results

We found significant differences in microclimate and soil moisture between microhabitat types. We detected the highest average and

Table 1
Soil moisture and microclimate differences between microhabitat types. Results of the Tukey type posthoc tests, z values are given. Grassl: grassland.

	Mean temp.	Max. temp	Min. temp	Mean hum.	Soil moisture
Forest - Edge	-2.694*	-3.190**	2.563	0.847	2.689*
Grassl.-Edge	12.188***	5.549***	-5.368***	-6.653***	-1.391
Dwarf shrub - Edge	6.417***	3.610**	0.027	-1.029	1.165
Grassl. - Forest	14.882***	8.739***	2.805*	-7.500***	-4.081***
Dwarf shrub - Forest	9.111***	6.800***	-2.526	-1.875	-1.524
Dwarf shrub - Grassl.	-5.771***	-1.939	5.331***	5.624***	2.556

Significance levels: *: <0.05, **: <0.01, ***: <0.001.

maximum temperatures in grasslands, and the coolest microhabitats were forests (Fig. 2A,B). We also detected the highest minimum temperature in grasslands with high variation between sites (Fig. 2C). We measured the highest soil moisture and air humidity values in forests, and the lowest ones in grasslands (Table 1, Fig. 2D,E).

We collected 3,588 adult spiders of 88 species (see Appendix A.). The most abundant species were *Arctosa lutetiana* (Simon, 1876), *Pardosa alacris* (C. L. Koch, 1833), *Zodarion germanicum* (C. L. Koch, 1837), which are all warm preferring species. We detected overlapping but separate species composition of microhabitat types according to NMDS (Fig. 3) and perMANOVA ($F = 12.73$, $p < 0.001$). Furthermore, all microhabitats had significantly different community compositions according to the pairwise perMANOVA tests ($p < 0.001$). Indicator species analysis indicated three species for forests, six for edges, one for grasslands and one for dwarf shrub microhabitats (see Appendix B).

Forests and edges had the highest species richness, followed by dwarf shrubs and grasslands with the lowest species richness (Fig. 4A, Table 2). We collected the highest abundance of high strata preferring species in the dwarf bushes (Fig. 4B, Table 2). Humidity preference of species followed the order of forests, edges, dwarf shrubs and grasslands (Fig. 4C, Table 2). The highest shading preference values were detected in the forests, followed by the edges, whereas the lowest values were detected in dwarf shrubs and grasslands (Fig. 4D, Table 2). We detected larger spiders at the edges compared to the dwarf shrub microhabitats (Fig. 4E Table 2).

Discussion

We found that forest-steppe forests, edges, grasslands and dwarf shrubs differ in their microclimate and spider fauna. Dwarf shrubs create a distinct microhabitat in forest steppe grasslands providing a cooler and moister microclimate than the surrounding grassland. Furthermore, we found a distinct spider community composition and trait state composition of spiders in forests, edges, grasslands and dwarf shrub microhabitats.

The canopy of woody structures reduces solar radiation. We measured about 2 °C lower temperature values under the shrubs than on the grasslands. Forests and edges were the coolest, with approximately 5 °C lower temperatures than open grasslands. This cooling effect is greater than the 2.1 °C summer cooling of forests predicted by a Europe-wide study (Haesen et al., 2021), presumably because of our studied forest steppes' relatively warm and dry climate. This aligns with De Frenne et al. (2019), who found that the cooling of mean and maximum temperatures in forests is the highest under warm climates. Furthermore, the large canopy of poplar trees shaded the ground level, and the thick canopy maintained a more temperate microclimate throughout the day and night due to thermal insulation (De Frenne et al., 2019). The difference between mean maximum and minimum temperatures was 11 °C in forests, whereas it exceeded 21 °C in grasslands, similar to dwarf shrub microhabitats. The thermal amelioration of forests and dwarf shrubs may foster species acclimated to cooler temperatures and lower thermal variation than the surrounding grasslands (Brigham & Suding, 2023).

The soil moisture and air humidity reducing effect was presumably levelled up by the wind-shading impact of the dwarf shrubs that decreased the wind desiccation underneath the canopy in the studied dry forest steppes (de Toma et al., 2022). Furthermore, we found significantly lower temperature in dwarf shrub habitats that might have reduced the evaporation rate compared to open grasslands. Wind-shading and temperature effects were more pronounced in the forests than in the dwarf shrub habitats, resulting in the coolest and most humid microclimate. The thermal optimum for arthropods is above 20 °C, and the critical maximum temperature is around 40 °C (Kearney et al., 2009). Therefore, the primary thermal challenge for arthropods in habitats with warm climates is to avoid high body temperatures. They might buffer the impact of climate change through physiological and behavioural adaptations, such as altered daily and seasonal activity (Kearney et al., 2009). Arthropods might reduce activity considerably during the middle of the day in the warm summer months (Deutsch et al. 2008). The efficacy of behavioural thermoregulation is related to the availability of a cool microhabitat, as the body temperature of arthropods is driven mainly by conductive heat exchange with nearby substances. Forest patches and, on a smaller scale, dwarf shrubs scattered on grasslands may provide shade and in turn, a relatively cool and moist shelter for arthropods during the hot summer days. The thermal heterogeneity created by woody vegetation allows arthropods to buffer

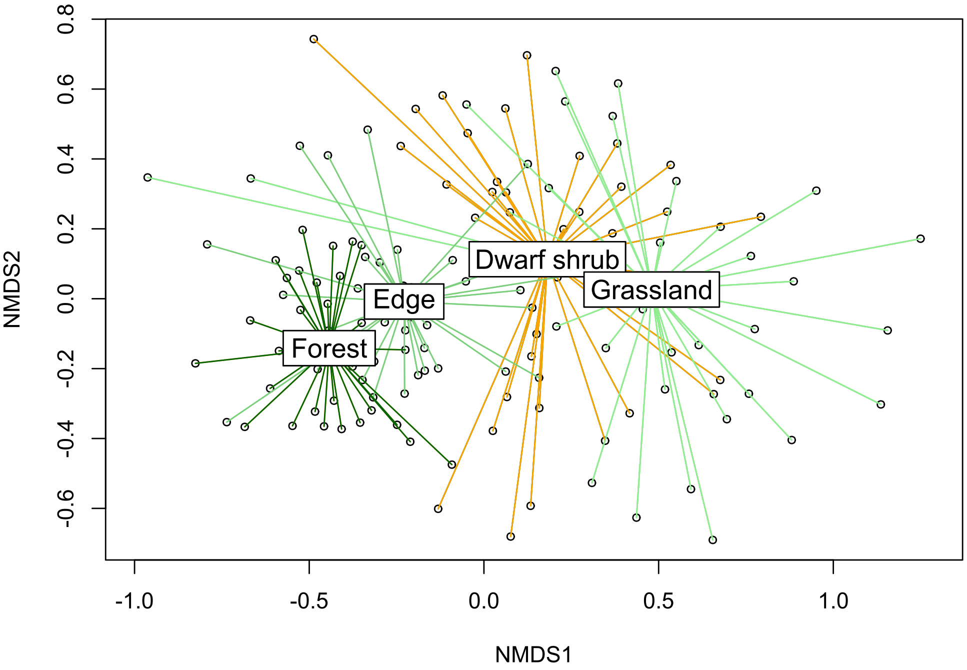

Fig. 3. Non-metric multidimensional scaling ordination (NMDS) of spider community composition. Sites are indicated with open circles. Labels are displayed in the centroids of sites of the microhabitat type.

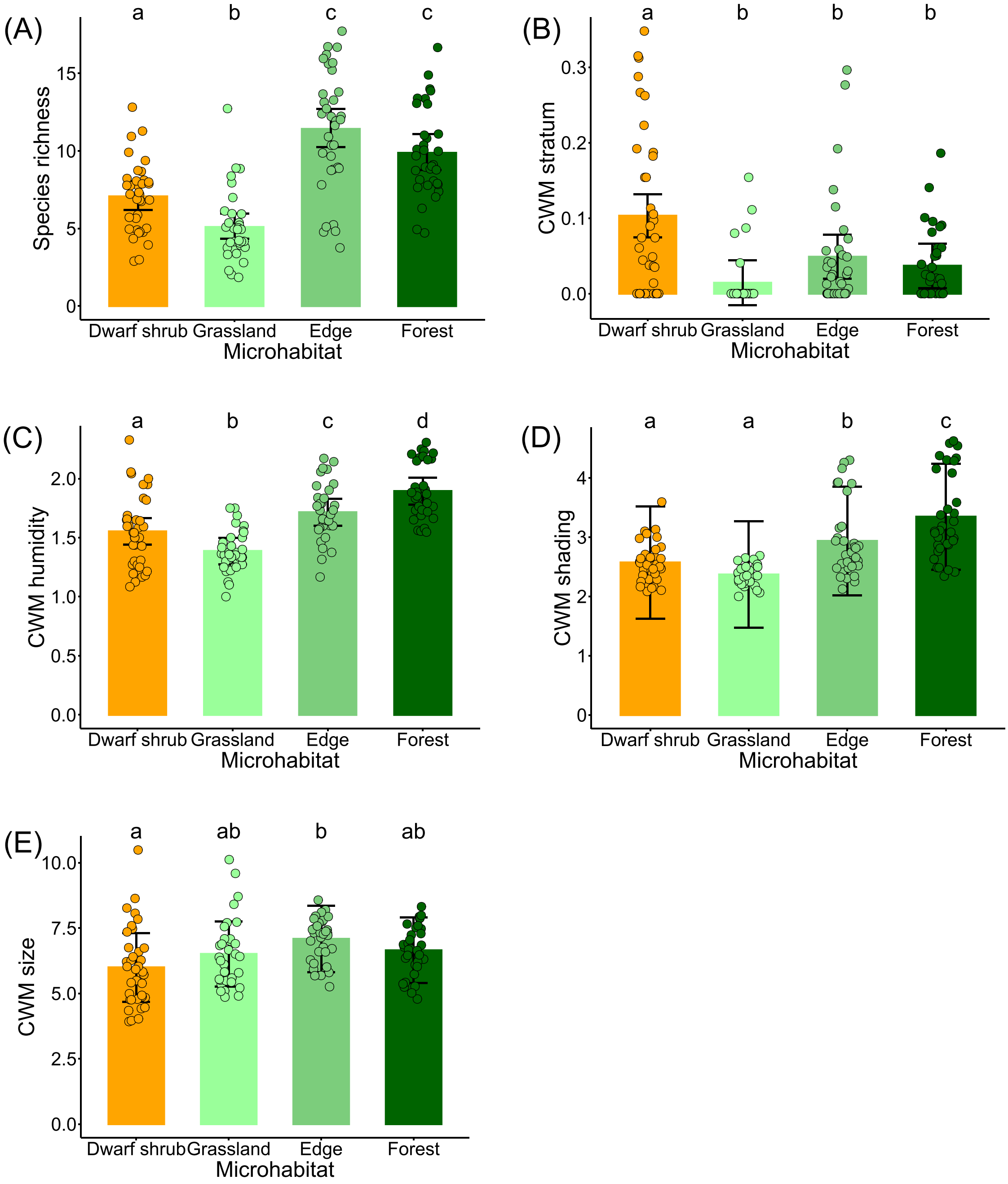

Fig. 4. Species richness and trait state composition of microhabitat types. (A) Species richness of spider communities, (B) CWM of stratum preference, (C) CWM of humidity preference, (D) CWM of shading preference, and (E) CWM of spider size. Bars represent estimated means, error bars are estimated 95% confidence intervals. Significant differences are indicated by different letters ($p < 0.05$).

extreme temperatures through behavioural thermoregulation (Pincebourde & Woods, 2020) and, in turn may alter the species compostion of spiders as found in the present study.

We showed that forests and edges hosted a higher species richness than grasslands and dwarf shrubs as a result of structural and microclimatic differences. Nevertheless, each microhabitat hosted a distinct community composition with numerous significant indicator species. Gallé et al. (2018, 2022) observed a similar pattern in dry forest steppes. Xeric grasslands formed on sandy soil with weak water-holding capacity and low humus content have relatively scarce vegetation dominated by xerotolerant perennial grasses, such as *Festuca vaginata* and *Stypa capillata*. The harsh microclimate and scarce vegetation have an environmental filtering effect on the fauna. Only xero- and thermotolerant spiders can survive these harsh microclimatic conditions, which results in a highly specialised grassland fauna with lower species richness than in the other microhabitats.

We found the most marked differences in the spider's shading and humidity preference between sites. Light condition is among the main factors for spider community composition in Central European lowland habitats (Entling et al., 2007; Muff et al. 2009). Spiders' small-scale distribution is strongly affected by the shading of woody plants (Gallé et al., 2022; Muff et al., 2009). We did not detect more spiders with a preference for shading in dwarf shrub microhabitats than in grasslands. However, the spider fauna in our relatively small forest patches included many forest species.

Soil moisture and air humidity are also among the most important

Table 2
Species richness and CWM value differences between microhabitat types. Results of the Tukey type posthoc tests, z values are given. Grassl: grassland,

	Species richness	Stratum preference	Humidity preference	Shading preference	Size
Forest - Edge	-1.929	-0.598	0.179*	0.409**	-0.438
Grassl.-Edge	-8.741***	-0.848	-0.328***	-0.566***	-0.577
Dwarf shrub - Edge	-5.955***	2.636*	-0.162*	-0.363**	-1.090***
Grassl. - Forest	-6.970***	-0.249	-0.507***	-0.975***	-0.138
Dwarf shrub - Forest	-3.998***	3.221**	-0.341***	-0.772***	-0.652
Dwarf shrub – Grassl.	3.298**	3.476**	0.165*	0.202	-0.513

Significance levels: *: <0.05, **: <0.01, ***: <0.001.

parameters influencing spiders (Entling et al., 2007), particularly in the dry grasslands of our study region (Gallé et al. 2023). Drought is expected to have the strongest impact on spiders during spring and early summer, the peak activity period of spiders (Buchholtz 2010b). Precipitation is also the highest in this period (Hungarian Meteorological Service, 2023). Sandy soils have high water infiltration and weak water-holding capacity (Ladányi et al., 2015). The reduced evaporation rate of shaded microhabitats compared to open grasslands retains water and creates a strong microscale moisture gradient during spring and early summer, our study period. This marked difference in moisture conditions affected spiders significantly. We observed a pronounced difference in the moisture preferences of spiders between microhabitats.

Dry and hot habitats, such as steppe grasslands, are assumed to favour large-bodied species because of their lower surface-to-volume ratio and, therefore, higher desiccation resistance (Entling et al., 2010). However, increased temperatures may result in increased metabolic costs and can be expected to lead to smaller body sizes (Scheffers et al., 2016). we found smaller spiders in dwarf shrubs than in edges. Spider size in forest steppes might be correlated with the available small invertebrates serving as food items for spiders, such as the high diversity of collembola in the edge microhabitats (Sławski & Sławska, 2000).

Besides microclimate, microhabitat structure also influences spiders (Langellotto & Denno, 2004; Lafage et al., 2019). Our results suggest that the spider communities are affected by vegetation structure, even when considering ground-dwelling species. Dwarf shrubs with high architectural complexity may support higher spider abundance and more species than structurally simple microhabitats (Spears & MacMahon, 2012). Structurally complex vegetation may allow more species to coexist by reducing inter-specific competition (Lafage et al., 2019). Furthermore, the amount of woody vegetation is positively associated with the quantity and depth of litter, a key variable in explaining species compositions of spider communities (Castro & Wise, 2009), particularly in poplar forests (Gallé et al., 2017). The small-scale microhabitat structures of small forest patches and dwarf shrubs created a mosaic habitat for spiders.

Willow species of the genus *Salix* produce a high diversity of specialised metabolites, mainly salicinoids that deter generalist herbivores (Denno et al., 1990). In fact, Kozel et al. (2022) found a relatively low herbivore abundance on rosmary-leaved willow bushes due to the large concentration of salicionid metabolites in the plants. The lower abundance of generalist herbivores might negatively affect the spider communities. However, in our study, spider species richness was higher in dwarf shrubs than in open grasslands. The negative effect of salicionid metabolites on generalist herbivores was presumably levelled up by a higher abundance of specialist herbivores and decomposers feeding on the litter of the dwarf shrub.

Climate change in the forest steppe region can be characterised as warming and drying. In the coming decades, drought frequency and severity will increase. Therefore, the climatic harshness of Eurasian forest steppes is projected to grow in the near future (Kröel-Dulay et al. 2022). Grassland vegetation is sensitive to humidity changes, whereas forest patches are influenced mainly by increasing temperature (You et al., 2021). Therefore, we expect an escalating positive effect of fine-scale woody structures on spiders.

Conclusions

Our study highlights the potential of heterogeneous microscale structures, such as dwarf-shrubs, in preserving arthropod communities under the ongoing climate change. Higher temperatures and more severe drought events will result in changes in species composition toward the dominance of dry and warm habitat specialists that can survive under extreme microclimatic conditions (Buchholz, 2010b). The future microclimate changes of small woody habitat features in the face of global warming and more extreme distribution of precipitation are mainly unknown (Shi et al., 2016; Pincebourde & Woods, 2020). Our results suggest that dwarf shrubs create a thermal heterogeneity that might aid arthropods in buffering macroclimatic warming through behavioural thermoregulation. They can support specialist species by forming connected networks of similar, buffered microclimates (Brigham & Suding, 2023).

CRediT authorship contribution statement

Róbert Gallé: Conceptualization, Formal analysis, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Nikolett Gallé-Szpisjak:** Data curation, Investigation, Methodology, Project administration, Visualization, Writing – review & editing. **Péter Batáry:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.09.006.

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